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Rhinochelys (Chelonioidea: Protostegidae) from the Late Cretaceous (Cenomanian) of Nammoura, Lebanon

Abstract - A new species of *Rhinochelys, R. nammourensis* n. sp. (Chelonioidea: Protostegidae), is described on the basis of beautifully preserved complete and articulated skeletons from the Nammoura locality, a Cenomanian (Late Cretaceous) Lagerstätte in Lebanon. Our study provides ontogenetic and front flipper characters for the family Protostegidae. Despite a very large ulnare, the front flipper of protostegids appears to retain the primitive digit configuration of chelonioids, in the relative length of the digits and phalanges and in the absence of reduction of the number of phalanges. The relative abundance of hatchling turtles suggests that Nammoura was near a nesting site during the Cenomanian.

Key words: Testudines, Protostegidae, Cretaceous, Cenomanian, Lebanon.

Riassunto - *Rhinochelys* (Chelonioidea: Protostegidae), del Cretacico superiore (Cenomaniano) di Nammoura, Libano.

Una nuova specie di *Rhinochelys*, *R. nammourensis* n. sp. (Chelonioidea: Protostegidae) viene descritta sulla base di scheletri completi e articolati in ottimo stato di conservazione provenienti dalla località di Nammoura, Lagerstätte cenomaniano (Cretacico superiore) del Libano. Lo studio fornisce caratteri ontogenetici e della natatoia anteriore per la famiglia Protostegidae. Nonostante un ulnare molto sviluppato, la natatoia anteriore dei protostegidi conserva apparentemente la configurazione primitiva delle dita nella relativa lunghezza delle dita stesse e delle falangi e nell'assenza di riduzione del numero di falangi. La relativa abbondanza di neonati suggerisce che nel Cenomaniano Nammoura era nelle vicinanze di un sito di nidificazione.

Parole chiave: Testudines, Protostegidae, Cretacico, Cenomaniano, Libano.

Introduction

The Nammoura locality is situated about 25 km northeast of Beirut, near the village of Nammoura, Kesrouâune Caza, in the region of Mont-Liban. The site consists of two quarries opened in the Al Gabour valley. The narrow and deep val-

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ley tends SEE-NWW and cuts a succession of Cretaceous limestones. The fossiliferous beds are dated as Cenomanian on the basis of the fauna of rudists, oysters and foraminifera, and the lower part of the succession, where the vertebrate remains come from, is of late Middle Cenomanian age (Dalla Vecchia *et al.*, 2002). Dalla Vecchia *et al.* divided the Cenomanian section of Nammoura into eight lithological units. The reptiles and birds are all from subunit 3b in the upper quarry. The rock of this unit is "pale blue-grey to greenish (pale yellow to beige when strongly weathered) 'lithographic' limestones with tabular bedding and plane parallel lamination" (Dalla Vecchia *et al.*, 2002). The macrofossils are rather rare there, well-preserved vertebrate remains are occasionally found by quarrymen, including fishes (Gayet, 1988; Bannikov & Bacchia, 2000; Belouze *et al.*, 2003; Forey *et al.*, 2003; Gayet *et al.*, 2003), dolichosaur varanoids (Dal Sasso & Pinna, 1997; Dal Sasso & Renesto, 1999), hindlimbed snakes (Rage & Escuillié, 2000, 2002, 2003; Rieppel & Head, 2004), theropod dinosaurs (Dalla Vecchia *et al.*, 2002), pterosaurs (Dalla Vecchia *et al.*, 2001) and birds (Dalla Vecchia & Chiappe, 2002). In addition to vertebrates, plants (Krassilov & Bacchia, 2000; Barale *et al.*, 2004) and insects (Nel *et al.*, 2004) are also reported. Turtle remains prevaile among reptiles at Nammoura (Dalla Vecchia & Venturini, 1999; Dalla Vecchia *et al.*, 2002), but hitherto no systematic study has been conducted.

The site of Nammoura is a "Konservat Lagerstätte" formed in a small and shallow marine basin with restricted water circulation in a carbonate platform. The relatively abundant representatives of terrestrial fauna and flora suggest that Nammoura during the Cenomanian was close to a land area, probably emergent islands (Dalla Vecchia *et al.*, 2002; Forey *et al.*, 2003) since the main continental coastline was several hundreds of kilometres to the south (Philip *et al.*, 2000). The prevalence of xeromorphic plants suggests an arid climate (Krassilov & Bacchia, 2000), which is in agreement with the hypothesized hypersalinity at the bottom of the basin where the Lagerstätte formed, suggested by the preservation of soft-tissues in vertebrate remains and the presence of needle-like crystals covering some fossil leaves (Dalla Vecchia *et al.*, 2002).

Here, we report on turtles from Nammoura. These turtle remains, comprising mostly beautifully preserved complete or partial articulated skeletons, as well as isolated elements, belong to a new species of *Rhinochelys* (Chelonioidea: Protostegidae). For the first time hatchling, juvenile and adult specimens of a single taxon of Protostegidae are reported. The purpose of the present paper is to give a detailed systematic description and to discuss the flipper characters of the family Protostegidae, as well as ontogenetic features. All fossils have been collected by quarrymen and private collectors. The type specimen of the new species is housed in the Museo Civico di Storia Naturale di Milano, Italy, and other specimens belong to the private collections of E. Makhoul, Beirut (Lebanon) and F. Escuillié, Gannat (France).

Institutional abbreviations

BMNH: Natural History Museum (London); MSNM: Museo Civico di Storia Naturale di Milano, Italy.

Systematic Paleontology

Chelonioidea Agassiz, 1857
Protostegidae Cope, 1872
Rhinochelys Seeley, 1869

Type species: *Rhinochelys pulchriceps* (Owen, 1842)
Revised diagnosis: protostegid with a large nasal bone and a laterally expanded and swollen skull roof at the prefrontal level.

Rhinochelys nammourensis n. sp.
(Figs. 1 – 8, 10)

Derivatio nominis: from the name of the locality where the turtle remains come from.
Holotype: an almost complete skeleton (MSNM V3933 (Figs. 1- 2, 4), Museo Civico di Storia Naturale di Milano, Italy).
Hypodigm: private collection of E. Makhoul, Lebanon: skeleton of neonate on two slabs (Ntu-1a&b), fragment of carapace with two neurals and two costals (Ntu-2), incomplete plastron (Ntu-3), flipper (Ntu-4), nearly complete carapace (Ntu-6) and two skeletons of neonate (Ntu-7 and Ntu-8); private collection of F. Escuillié, France: skeleton of adult with nearly complete carapace, forelimbs, partial hindlimbs, neck and tail, lacking skull (ESC-2) and skeleton of neonate (ESC-3).
Locus typicus: Nammoura, Lebanon.
Stratum typicum: Cenomanian, Late Cretaceous.
Diagnosis: a species of *Rhinochelys*, differing from *R. pulchriceps* in having a narrower skull, a smaller nasal, a smaller frontal with a narrower and longer anterior process, a longer and narrower parietal, a single suprapygal plate, and the width of the second to fourth vertebral scutes increasing from front to back.
Measurements: see Tab. 1.

Tab. 1 - Measurements of *Rhinochelys nammourensis* n. sp., from the Cenomanian (Late Cretaceous) of Nammoura, Lebanon (in mm).
Tab. 1 - Misure di *Rhinochelys nammourensis* n. sp., del Cenomaniano (Cretacico superiore) di Nammoura, Libano (in mm).

	skull		shell	
	Length	Width	Length	Width
MM V3933	60	30	124	(98)
Ntu-6	—	—	125	(93)
Ntu-1	—	—	16	19
Ntu-7	10	9	21	21
Ntu-8	12	10	18	18
ESC-3	14	10	17	17
ESC-2	—	—	270	212

( ) : estimated.

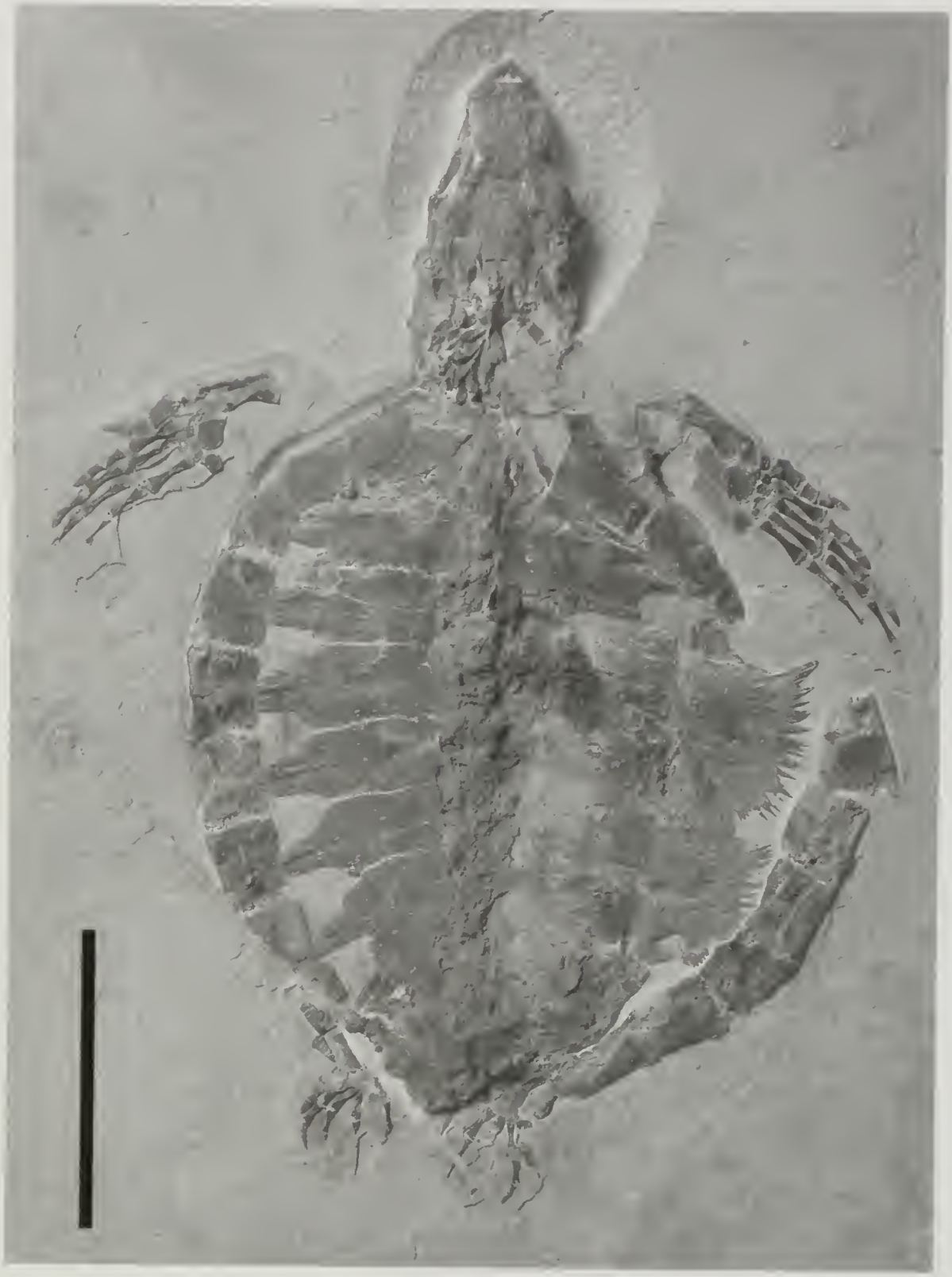

Fig. 1 - *Rhinochelys nammourensis* n. sp.: MSNM V3933, holotype (olotipo), Cenomanian (Late Cretaceous) of Nammoura, Lebanon (Cenomaniano (Cretacico superiore) di Nammoura, Libano). Skeleton in dorsal view (Scheletro in norma dorsale). Scale bar (Scala metrica) = 50 mm.

Description and comparisons

Skull (Figs. 1-3)

Preservation

The skull is preserved in MSNM V3933, Ntu-7, Ntu-8 and ESC-3. In MSNM V3933, it is nearly complete and visible in dorsal view (Fig. 2). The surface of the skull roof between the orbits is damaged, and the skull is crushed dorsoventrally, and slightly laterally as well. The skull of Ntu-7 is incomplete. It is exposed in dorsal view and lacks the skull roof (Fig. 3D). Ntu-8 is damaged and exposed in ventral view (Fig. 3C). The skull of ESC-3 is almost complete and exposed in dorsal view (Fig. 3A-B). The detailed description is based on MSNM V3933 (Figs. 1 and 2). The hatchling specimens are compared to MSNM V3933.

MSNM V3933

The skull has a roughly triangular shape as seen from above, with the lateral margins posterior to the orbits parallel to each other. The snout is pointed. The skull roof at the prefrontal level is laterally expanded, as in *Rhinochelys pulchriceps* (Collins,

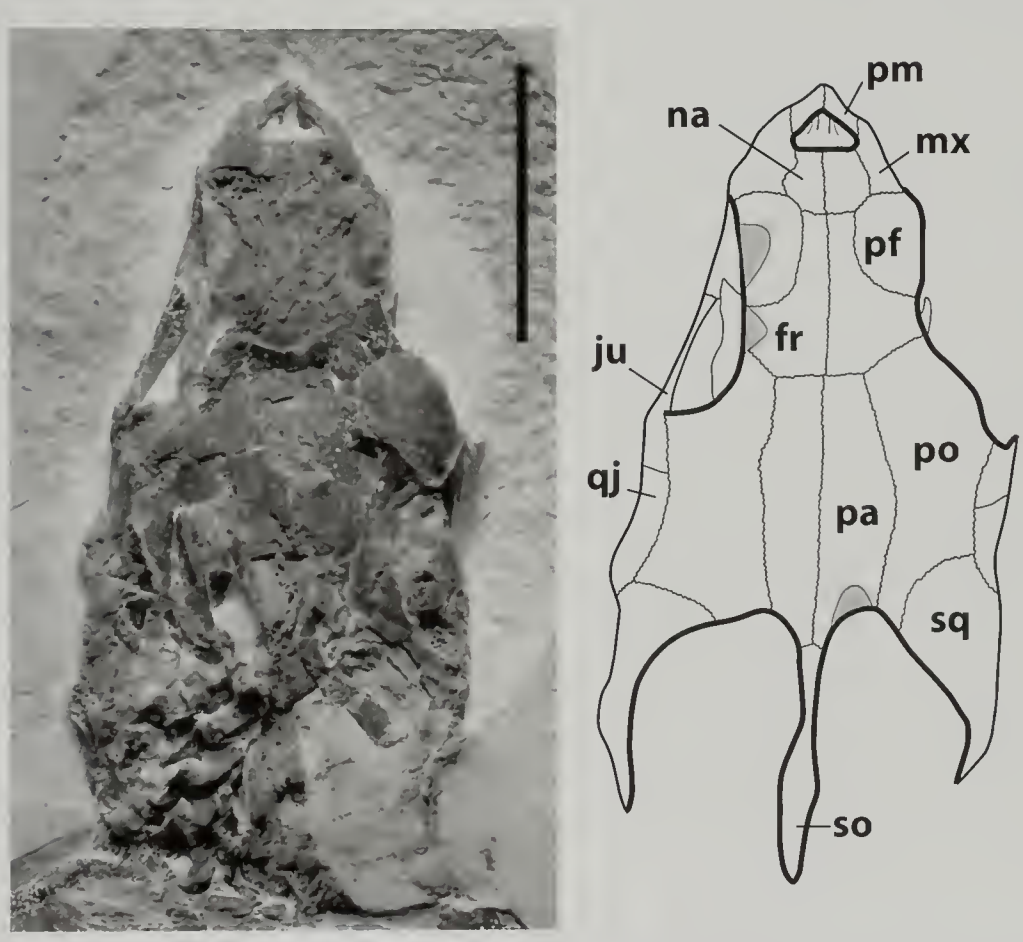

Fig. 2 - *Rhinochelys nammourensis* n. sp.: MSNM V3933, holotype (olotipo), Cenomanian (Late Cretaceous) of Nammoura, Lebanon (Cenomaniano (Cretacico superiore) di Nammoura, Libano). Detail of skull in dorsal view (Particolare del cranio in norma dorsale). Scale bar (Scala metrica) = 20 mm. fr: frontal (frontale); ju: jugal (iugale); mx: maxilla (mascellare); na: nasal (nasale); pa: parietal (parietale); pf: prefrontal (prefrontale); pm: premaxilla (premascellare); po: postorbital (postorbitale); qj: quadratojugal (quadratoiugale); so: supraoccipital (sopraoccipitale); sq: squamosal (squamoso).

1970; Hirayama, 1994). The orbit is large and mainly directed laterally. The posterior part of the skull, although crushed, shows a deep temporal emargination, which is much deeper than that in the reconstruction of *Rhinochelys pulchriceps* (Hirayama, 1994). The crista supraoccipitalis is very long.

Nasal: the anterior portion of both nasals is complete, but the surface of the posterior portion is damaged. The nasal is a large bone, which is about half the size of the prefrontal. It is an anteroposteriorly elongate element forming the upper rim of the apertura narium externa. Anterolaterally, the nasal/maxilla suture is well preserved. Posterolaterally, the nasal contacts the prefrontal. Posteriorly, the nasal meets the frontal, preventing the prefrontals from meeting one another on the midline.

The nasal is absent in derived Cheloniidae and in Dermochelyidae, but still present in primitive cheloniids, such as *Toxochelys latiremis* and *Porthochelys laticeps*, in which a pair of small nasals is present (Zangerl, 1953b). Among Protostegidae, a relatively large nasal, at least half the size of the prefrontal, is present only in *Rhinochelys pulchriceps* and *Desmatochelys lowi* (Williston, 1898; Collins, 1970; Hirayama, 1994; Elliot *et al.*, 1997), while *Santanachelys gaffneyi* (Hirayama, 1998), *Notochelone costata* (Hirayama, unpublished data), and *Chelosphargis advesa* (Hirayama, 1994) have a much smaller nasal, less than one third the size of the prefrontal. The nasal is absent in advanced protostegids, such as *Protostega gigas* (Wieland, 1906) and *Archelon ischyros* (Wieland, 1900a, 1909). The nasal of *Rhinochelys pulchriceps*, however, is as large as the prefrontal, larger than in MSNM V3933 and *Desmatochelys lowi* (Hirayama, 1994).

Prefrontal: the left prefrontal is damaged, and although the outline of the right one is complete, parts of its surface are damaged. The prefrontal forms the anterior part of the upper margin of the orbit, along which it is laterally expanded and swollen, as in *Rhinochelys pulchriceps* (Collins, 1970; Hirayama, 1994). The prefrontal contacts the maxilla anteriorly by a nearly transverse suture. Anteromedially, it contacts the nasal and posteromedially the frontal. The prefrontals do not contact one another along the midline, as in most protostegids, including *Santanachelys gaffneyi*, *Rhinochelys pulchriceps* and *Desmatochelys lowi*. In advanced protostegids (*Archelon isclıyros* and *Protostega gigas*), the prefrontals meet one another along the midline.

Premaxilla: only the dorsal side and part of the anterior surface of both premaxillae are visible. The premaxilla forms the lower rim of the apertura narium externa and contacts the maxilla posterolaterally.

Maxilla: the maxilla is visible only dorsally and laterally. It forms the lateral rim of the apertura narium externa, the anterior rim, and the anterior portion of the lower rim of the orbit. On the skull roof, the maxilla contacts the nasal medially and the prefrontal posteriorly. The maxilla/jugal contact is visible on the left side, on the floor of the orbit.

Frontal: the surface of both frontals is damaged, but the right frontal is more complete. The morphology and contacts of the frontal in MSNM V3933 are similar to those of *Santanachelys gaffneyi* and *Rhinochelys pulchriceps*. The frontal forms a small portion of the upper rim of the orbit between the prefrontal and the postorbital, as in *Santanachelys gaffneyi*, *Rhinochely pulchriceps* and *Desmatochelys lowi*. In *Archelon ischyros* and *Protostega gigas*, the frontal does

not reach the orbital margin. The frontal contacts the nasal anteriorly by a short suture, the prefrontal anterolaterally, the parietal posteriorly and the postorbital posterolaterally. The frontal in MSNM V3933 appears to be smaller than that of *Rhinochelys pulchriceps* and its anterior portion is narrower than in the latter.

Postorbital: both postorbitals are complete but crushed. The postorbital is an anteroposteriorly elongate element forming the posterior rim of the orbit. It contacts the frontal anteromedially by a short suture, the parietal medially by a long suture, the jugal anterolaterally, the quadratojugal posterolaterally and the squamosal posteriorly. Posteriorly, the postorbital forms a small portion of the temporal emargination, separating the parietal from the squamosal, as in *Santanachelys gaffneyi, Rhinochelys pulchriceps* and *Desmatochelys lowi*. In *Archelon ischyros*, *Protostega gigas*, dermochelyids and most cheloniids, the postorbital does not reach the temporal emargination.

Parietal: both parietals are complete but crushed. The parietal is an anteroposteriorly elongate bone, which appears to be longer and narrower than that of *R. pulchriceps*. It forms the medial portion of the temporal emargination and contacts the frontal anteriorly, the postorbital laterally and the supraoccipital posteriorly by a short suture. The parietal/squamosal contact is absent as in *Santanachelys gaffneyi*, *Rhinochelys pulchriceps* and *Desmatochelys lowi*, while this contact is present in most Cheloniidae, Dermochelyidae, *Archelon ischyros* and *Protostega gigas*.

Quadratojugal: only the upper part of the quadratojugal is visible on both sides between the jugal and the squamosal. It contacts the postorbital medially.

Jugal: the jugal is preserved on both sides but only the upper part is visible. It forms the posteroventral margin of the orbit and contacts the postorbital medially, the quadratojugal posteriorly and the maxilla anteriorly. The jugal has no medial process, as in the other protostegids (Hirayama, 1998).

Squamosal: of the two squamosals, the right one is better preserved. This is a triangular element as seen from above. It forms the lateral portion of the temporal emargination, contacting the postorbital anteromedially and the quadratojugal anterolaterally. The squamosal of MSNM V3933 is similar to that of *Santanachelys gaffneyi* in shape, but it is clearly larger than in the latter. *Desmatochelys lowi*, *Protostega gigas* and *Archelon ischyros* also have a larger squamosal, like MSNM V3933, this bone is however wider in dorsal view in these forms than in MSNM V3933. The squamosal is not preserved in *Rhinochelys pulchriceps*; the reconstruction of the skull by Hirayama (1994) shows a small squamosal, which is similar to that of *Santanachelys gaffneyi* in size.

Supraoccipital: the supraoccipital is complete but somewhat deformed. It is an anteroposteriorly elongate element as seen from above. It forms the crista supraoccipitalis and contacts the parietals anteriorly. The crista supraoccipitalis is very long, being longer than that of *Santanachelys gaffneyi*. This structure is not preserved in *Rhinochelys pulchriceps*.

The skull scute sulci are not distinguishable because of the crushing of the skull roof. Other elements of the skull are not visible at the present state of the preparation.

Hyoid bone: the posterior portion of the cornu branchiale I is visible on the right side of MSNM V3933. It is curved with the posterior end flattened.

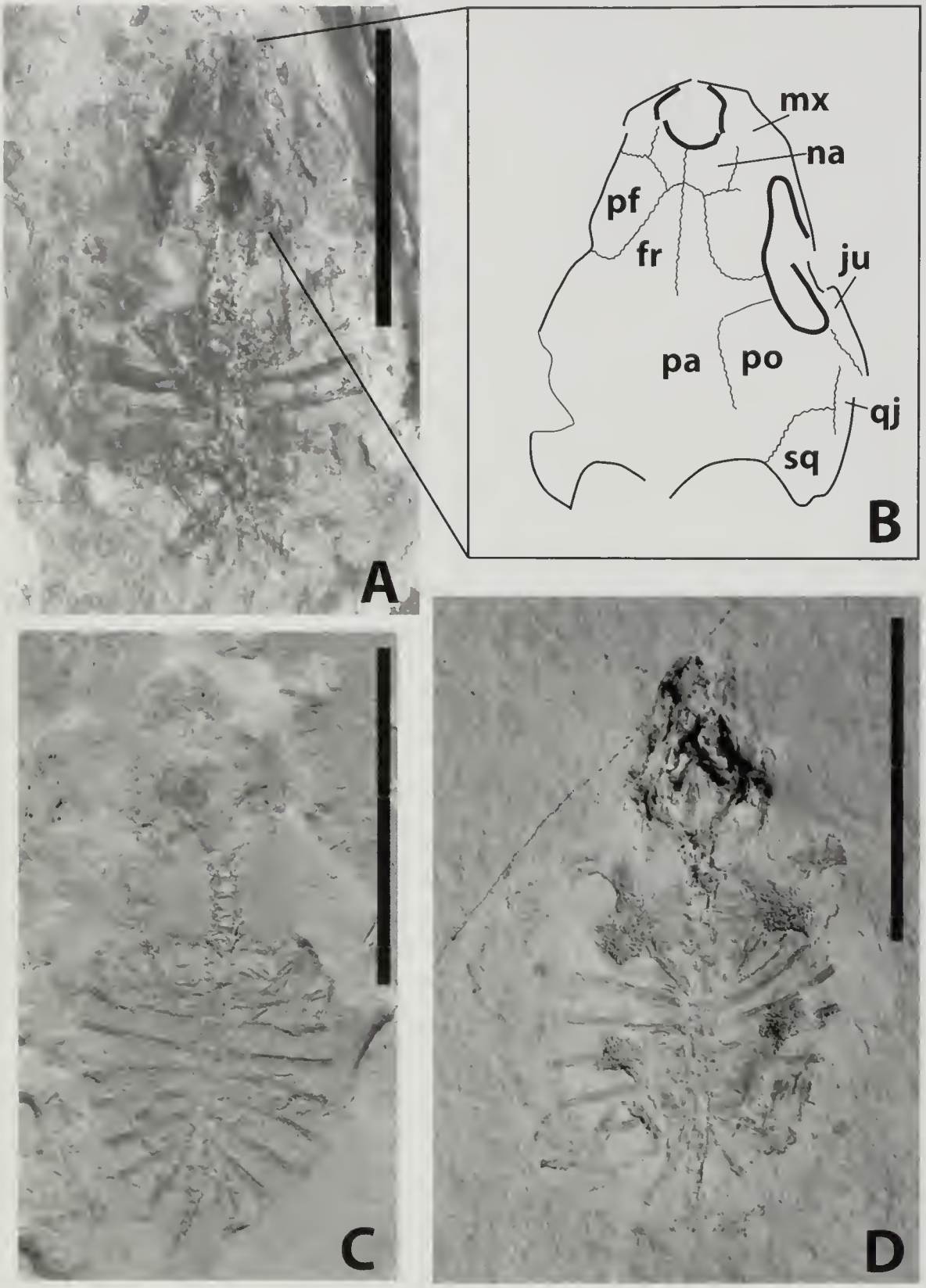

Fig. 3 - *Rhinochelys nammourensis* n. sp., Cenomanian (Late Cretaceous) of Nammoura, Lebanon (Cenomaniano (Cretacico superiore) di Nammoura, Libano). Skeleton of hatchlings (Scheletro di neonati). A) ESC-3 in dorsal view (in norma dorsale); B) Key for skull of ESC-3 (Legenda del cranio di ESC-3); C) Ntu-8; D) Ntu-7. Scale bar (Scala metrica) = 20 mm. Abbreviations: see Fig. 2 (Abbreviazioni come in Fig. 2).

Hatchling specimens

The skull of hatchling specimens Ntu-7, Ntu-8 and ESC-3 is large relative to the shell and rather wide as seen in other neonate turtles. Ntu-7 and ESC-3 are visible in dorsal view, ESC-3 has the skull roof partly preserved while in Ntu-7 the skull roof is damaged. The overall shape of the skull of these hatchlings, as seen from above, is similar to that of MSNM V3933, the skull margins posterior to the orbit being parallel to each another and the anterior part of the skull roof being laterally expanded. The morphology and the relationships of the skull elements, including the maxilla, nasal, prefrontal, frontal, postorbital, squamosal, jugal and quadratojugal in ESC-3 are similar to those of MSNM V3933 (Fig. 3).

Shell (Figs. 1 and 3-7)

Preservation: in MSNM V3933, the left half of the carapace is well preserved with the plates *in situ*, while most of the right half including the second to eighth costal plates is missing and the remaining peripherals are pushed laterally. This exposes most of the right half of the plastron, which is slightly pushed laterally, in dorsal view (Fig. 1 and 4). The carapace of Ntu-6 is exposed in dorsal view, but it lacks most of the peripheral plates (Fig. 5). The almost complete carapace and plastron are preserved in the slab and counterslab of hatchling specimen Ntu-1 (Fig. 7). The carapace and plastron are exposed in dorsal view in hatchling specimens Ntu-7 and ESC-3 and in ventral view in Ntu-8 (Fig. 3). The complete carapace is exposed in ventral view in ESC-2 (Fig. 6).

Fig. 4 - *Rhinochelys nammourensis* n. sp.: MSNM V3933, holotype (olotipo), Cenomanian (Late Cretaceous) of Nammoura, Lebanon (Cenomaniano (Cretacico superiore) di Nammoura, Libano). Carapace in dorsal view (Carapace in norma dorsale). Scale bar (Scala metrica) = 50 mm.

Carapace: in the juvenile specimens MSNM V3933 (Figs. 1 and 4) and Ntu-6 (Fig. 5), the carapace has an oval outline. The surfaces of all neurals are damaged on both MSNM V3933 and Ntu-6, although a midline elevation or keel can be observed that stretches from the nuchal to the suprapygal. Whether the keel exhibited knobs cannot be determined. The carapace has a roof-shaped cross section, as in *Rhinochelys* (*Cimochelys*) from the Albian to Turonian of southeast England (Mantell, 1841; Owen, 1842; Collins, 1970). Most of the carapace margin is smooth except for the posterior margin from the ninth peripheral to the pygal where it is undulated in MSNM V3933 and serrated in Ntu-6. A deep posterior notch is present on the pygal of Ntu-6. The posterior margin is not complete in MSNM V3933. The anterior margin of the carapace is nearly straight and the nuchal emargination is very shallow. Lateral carapacial fontanelles are present between the peripheral and costal plates in all specimens, even in the adults. The width of the fontanelles is about one third of the width of the costal plates in MSNM V3933, but they are wider in Ntu-6. The carapace surface is not perfectly smooth: the peripheral plates are covered with fine ridges radiating from the centre of each plate, and the lateral portion of the costals bears straight transverse and parallel ridges. These ridges are possibly a juvenile feature, not found in other protostegids.

The nuchal is not complete in MSNM V3933, but its outline can be made out. This plate is preserved in Ntu-6, although somewhat deformed. The nuchal is trapezoidal in shape and wider posteriorly, its width being twice its length. The series of neurals is damaged on the surface in both MSNM V3933 and Ntu-6, but the interneural sutures are visible. Eight rectangular neurals are present, all longer than wide, the eighth one,

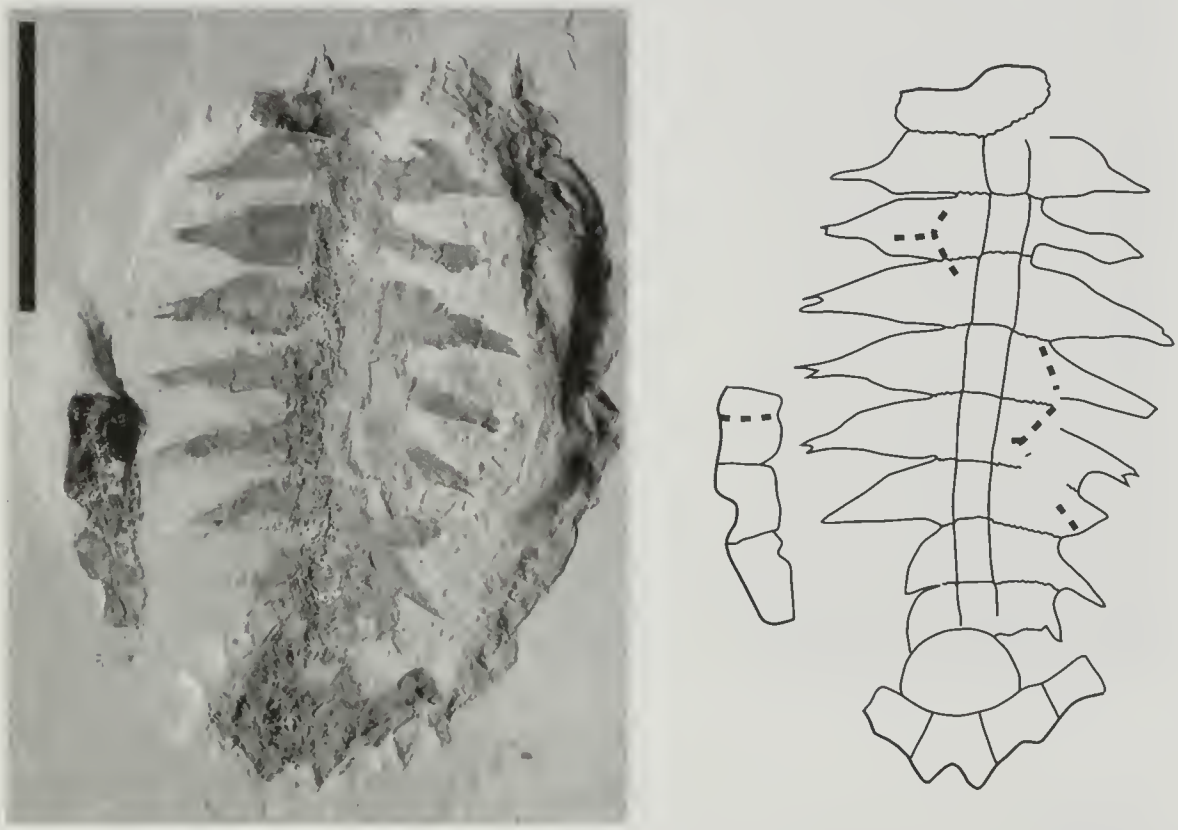

Fig. 5 - *Rhinochelys nammourensis* n. sp.: Ntu-6, Cenomanian (Late Cretaceous) of Nammoura, Lebanon (Cenomaniano (Cretacico superiore) di Nammoura, Libano). Carapace in dorsal view (Carapace in norma dorsale). Scale bar (Scala metrica) = 50 mm.

however, is shorter than the other neurals. There is one suprapygal as in most protostegids except for *Rhinochelys* (*Cimochleys*) and *Desmatochelys lowi* (Zangerl & Sloan, 1960; Collins, 1970; Hirayama, 1994, 1997). The suprapygal is large, roughly semicircular in shape and slightly wider than long. In *Rhinochelys* (*Cimochelys*), two suprapygals are present, the first one is trapezoidal or triangular and the second one is rectangular, wider than long and larger than the first suprapygal. Eight costal plates are present as in *Santanachelys gaffneyi* and *Rhinochelys* (*Cimochelys*), with the lateral portion narrowed to form a peg fitting into a socket on the peripheral. *Protostega gigas* and *Archelon ischyros* have nine more blade-like costals. The complete series of eleven peripherals is preserved on the left side of MSNM V3933. The first peripheral is roughly triangular and wider than long. The pygal plate is not complete in MSNM V3933, it is nearly complete in Ntu-6, but with the surface damaged on both. The pygal has a deep and wide notch on the posterior margin in Ntu-6. This is different from *Rhinochelys* (*Cimochelys*) in which such a notch is absent and the posterior end of the carapace is pointed (BM 28706 and BM 36751) as in all other protostegids, except for *Santanachelys gaffneyi* (Hirayama, 1994, 1997, 1998).

The scute sulci are weakly developed but partly discernable on MSNM V3933 and Ntu-6. The first, third and fourth vertebrals are wider than long while the second one is much longer than wide. The intervertebral sulci cross the first neural and costal, the third neural and costal, the fifth neural and costal and the eighth neural and costal plates respectively. The width of the second to fourth vertebrals increases strongly from front to back, with the lateral margins strongly angled. In *Rhinochelys* (*Cimochelys*), the scute sulci are more deeply printed than in the Nammoura turtles; the vertebral scutes extend to at least half the width of the costal plates and their width remains unchanged or becomes slightly smaller from front to back (Owen, 1842; Collins, 1970).

The carapace of adult specimen ESC-2 is slightly more elongate than in the juveniles and it is almost flat in ventral view. The carapace margin is smooth throughout. Although the posterior margin of the carapace is a little damaged, a posterior notch is apparently present on the pygal. This notch is shallower in ESC-2 than in the juveniles. The carapacial fontanelles are more closed than in the juveniles, being about one fourth of the width of the costal plates. The morphology of plates in ESC-2, including the nuchal, the neural series, the pygal and the peripherals is similar to those of the juveniles.

The hatchling specimens Ntu-1, Ntu-7, Ntu-8 and ESC-3 have a more rounded carapace than the juveniles. Their costals are blade-like and completely separated from one another by large fontanelles due to poor dermal ossification. No peripherals are preserved in Ntu-1, Ntu-8 and ESC-3. Some yellow spots are present around the carapace of Ntu-7 (Fig. 3D), however they seem not to be osseous.

Plastron: in MSNM V3933, the right part of the plastron, including the right hyoplastron, hypoplastron and xiphiplastron, is visible in dorsal view, through the damaged carapace. However, the anterior part of the plastron, including the epiplastron and entoplastron, is not visible. The hyoplastron and hypoplastron are large and star-shaped plates with short finger-like prongs which are well visible on the medial and lateral margins. The hypoplastron is smaller than the hyoplastron, as in *Archelon ischyros* and *Protostega gigas*. The hyoplastron contacts the hypoplastron by a long and strongly interdigitated suture. There is a large central fontanelle between the hyoplastra and hypoplastra. The central plastral fontanelle

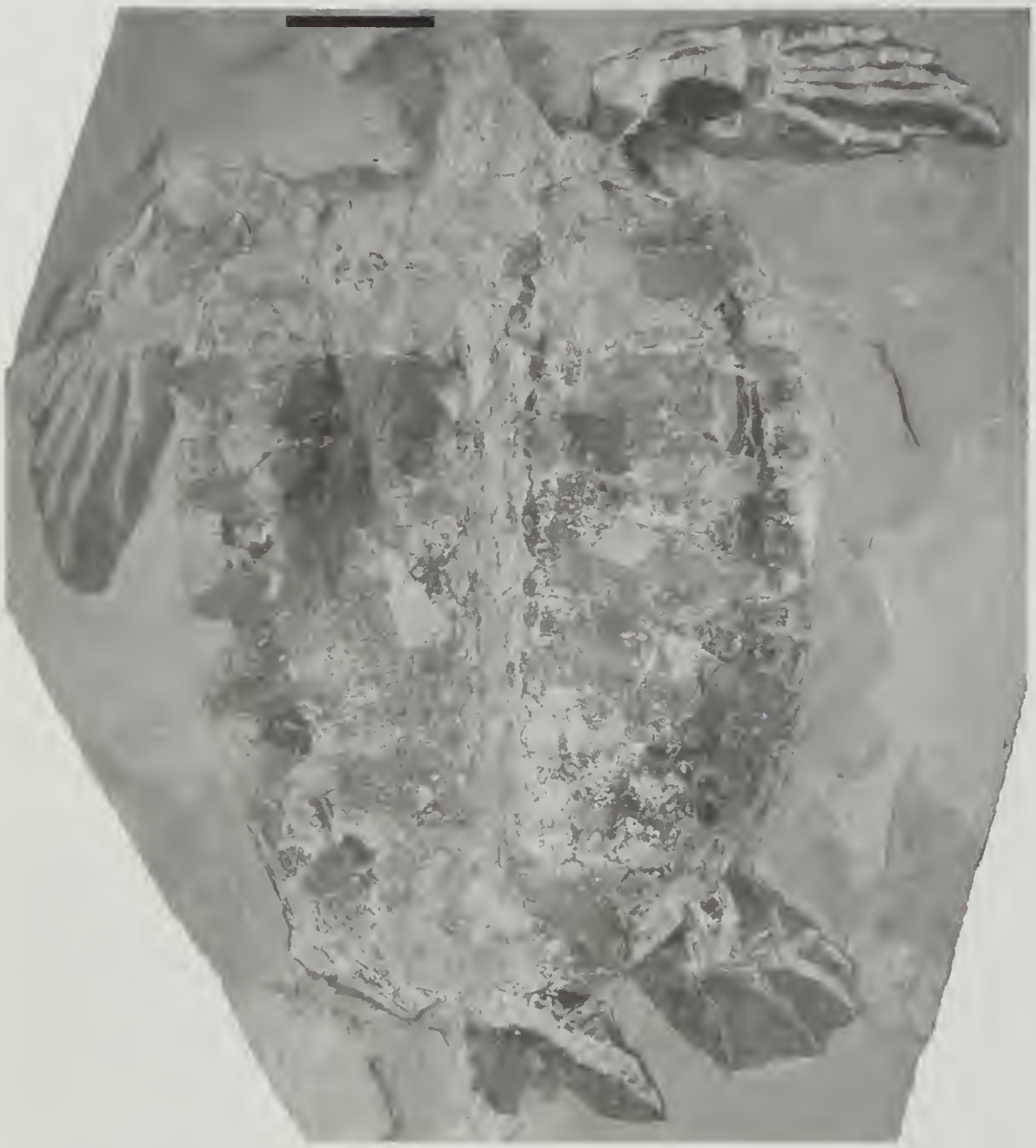

Fig. 6 - *Rhinochelys nammourensis* n. sp.: ESC-2, Cenomanian (Late Cretaceous) of Nammoura, Lebanon (Cenomaniano (Cretacico superiore) di Nammoura, Libano). Adult skeleton in ventral view (Scheletro di adulto in norma ventrale). Scale bar (Scala metrica) = 50 mm.

is smaller than the hypoplastron. The plastral index (axillary-inguinal notch distance/hyo-hypoplastral suture length x 100) is more than 100 as in all protostegids and dermochelyids (Zangerl, 1953b; Hirayama, 1998). The xiphiplastron is anteroposteriorly elongated and bends laterally as in other protostegids. The posterior part of the left xiphiplastron contacts the right one by an indented midline suture. The midline contact of the xiphiplastron in MSNM V3933 seems to be shorter than that of *Santanachelys gaffneyi*. In *S. gaffneyi*, the xiphiplastron contacts its counterpart for nearly all its length (Hirayama, 1998), while in the more advanced protostegids such as *Archelon ischyros* and *Protostega gagas*, the midline contact of the xiphiplastra is more reduced than in the Nammoura turtles (Zangerl, 1953a).

In the hatchling specimens Ntu-1a, the almost complete plastron is exposed in dorsal view. The plastron of Ntu-7, also exposed in dorsal view, is damaged. A partial plastron is preserved in Ntu-8 and exposed in ventral view. The position of the plastron is well anterior relative to the carapace: the anterior margin of the plastron appears to extend forward beyond the anterior margin of the carapace and the posterior margin of the hyoplastron is at the level of the first costal plate. This might be due to post-mortem deformation. The epiplastra, preserved in Ntu-1a, are blade-like elements. They are more reduced than those of *Santanachelys gaffneyi* (Hirayama, 1998). In *Archelon ischyros* and *Protostega gigas*, the epiplastron is fused to the entoplastron (Hirayama, 1994). The entoplastron, preserved in both Ntu-1a and Ntu-7, is T-shaped with distinctive lateral wings, as in other protostegids and dermochelyids (Hirayama, 1998). The hyoplastra and hypoplastra are separated from one another by a large fontanelle that spans the full width. The space between the hypoplastra and hyoplastra is equal to the length of the latter. The hyoplastron is roughly rectangular and much wider than long. The hypoplastron is smaller than the hyoplastron. The anterior, lateral and posterior margins of the hyoplastron and hypoplastron are smooth while the medial margin shows strong finger-like prongs. The xiphiplastra are anterolaterally-posteromedially elongated and bent laterally. The right xiphiplastron is separated from the left one by a series of large caudal vertebrae, this is at least partly due to post-mortem crushing. An indentation is present on the short medial margin of the xiphiplastron.

Fig. 7 - *Rhinochelys nammourensis* n. sp.: Ntu-1, Cenomanian (Late Cretaceous) of Nammoura, Lebanon (Cenomaniano (Cretacico superiore) di Nammoura, Libano). Skeleton of hatchling (Scheletro di neonato). Left (a sinistra): Ntu-1a in dorsal view (in norma dorsale); right (a destra): Ntu-1b in ventral view (in norma ventrale). Scale bar (Scala metrica) = 20 mm.

Vertebral column

Cervical vertebrae: four cervical vertebrae are visible in MSNM V3933, exposed in lateral view. Only the neural arches are visible, showing strong zygapophyses. A series of articulated cervicals is preserved in Ntu-1, mostly in Ntu-1b, exposed in ventrolateral view. As in other chelonioid sea turtles, the centra are stout and short. The best preserved vertebral centra, the 5^{th} to 7^{th} ones, show a slight ventral keel. In Ntu-7, Ntu-8, ESC-3 and ESC-2, the cervical vertebrae are preserved but they are either crushed or damaged. There is no articular surface exposed.

Caudal vertebrae: no caudal vertebrae are visible in MSNM V3933. A series of fourteen articulated caudal vertebrae is preserved in ESC-2 and there are sixteen caudal vertebrae in Ntu-1. Caudal vertebrae are also preserved in Ntu-7, Ntu-8 and ESC-3, but they are damaged. The tail of ESC-2 is long, extending well beyond the posterior margin of the carapace, while that of hatchling Ntu-1 is short, extending barely beyond the posterior carapace margin. In both specimens, the centra are stout and short, their size decreases from front to back.

Pectoral girdle

The pectoral girdle is preserved only in the hatchlings, and is best preserved in Ntu-1. In this specimen, the blade-like coracoid is very long as in other advanced chelonioids. It is much longer than the humerus and extends posteromedially to the anterior margin of the hypoplastron. The scapular angle, formed by the acromion and the scapular prong, is about 120°.

Pelvic girdle

The pelvic girdle is visible only in hatchlings, but in a very bad condition. An accurate description is impossible.

Forelimb (Figs. 1, 6-8)

The forelimbs are preserved on both sides of MSNM V3933 and ESC-2. Ntu-4 is an isolated right front flipper, but most bones are missing, although their imprint is well preserved. Both forelimbs are preserved in Ntu-1. An incomplete left forelimb is preserved in Ntu-7. In Ntu-8, only the imprint of the right humerus is preserved.

Humerus: in the adult ESC-2, both humeri are damaged and exposed in ventral view. The right humerus is the better-preserved element and although its surface is damaged, the outline is preserved. The humerus is robust, with a straight shaft. The large medial process is taller than the caput humeri. The small lateral process is situated mid-way along the shaft of the humerus and is restricted to the anterior surface of the humeral shaft as in other protostegids (Hirayama, 1992). The posterior margin of the humeral shaft is strongly concave as in *Archelon ischyros* and *Protostega gigas* (Wieland, 1900b).

In the juvenile MSNM V3933, only the distal portion of the right humerus is visible. The distal end is expanded and the posterior margin of the humeral shaft is strongly concave as in ESC-2.

In the hatchling specimens, the humerus is nearly complete in Ntu-1a, but lack-

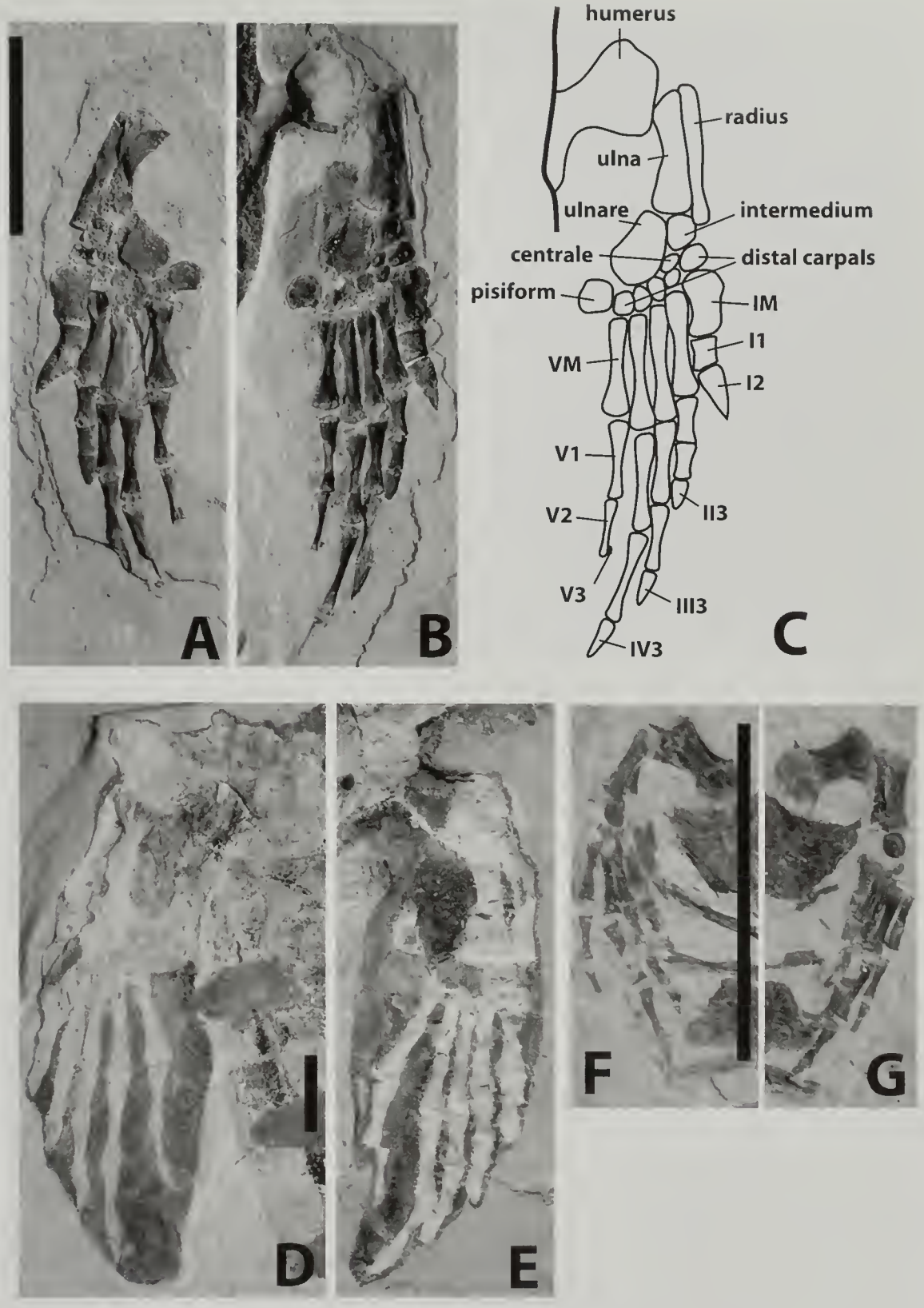

Fig. 8 - *Rhinochelys nammourensis* n. sp. from the Cenomanian (Late Cretaceous) of Nammoura, Lebanon (Cenomaniano (Cretacico superiore) di Nammoura, Libano). Detail of front flipper (Particolare della natatoia anteriore). A-C): MSNM V3933; D-E): ESC-2; F-G): Ntu-1a. Scale bar (Scala metrica) = 20 mm.

ing the caput humeri. In this specimen, the humerus is a rather short and robust bone, with a straight shaft and enlarged proximal and distal ends. The medial process is tall and the small lateral process is restricted to the anterior surface of the humeral shaft as in adult ESC-2. However its position appears to be more proximal.

Radius and ulna: these two bones are preserved in hatchlings, juveniles and adults. In all specimens, the radius is slightly longer than the ulna, its length is about 60 % of that of the humerus in adult specimen ESC-2 and 80% in hatchling specimen Ntu-1a. It is straight in Ntu-1a and very slightly bent anteriorly in hatchling Ntu-7 and both juveniles MSNM V3933 and Ntu-4. However, the curvature of the radius in the juvenile specimens is less than that of *Santanachelys gaffneyi* (Hirayama, 1998) and *Desmatochelys lowi* (Zangerl & Sloan, 1960). The adult specimen ESC-2 has a more pronounced anterior bending of the radius, which tends to form an elbow, but it is less pronounced than in *Archelon ischyros* and *Protostega gigas*. The ulna is a robust bone with wide proximal and distal ends, and a curved posterior border of the shaft.

Carpals, metacarpals and phalanges: the front flippers are best preserved in juvenile MSNM V3933. The length from the proximal end of the radius to the distal end of the fourth digit in MSNM V3933 is about half the length of the carapace. The juvenile specimens (MSNM V3933 and Ntu-4) have well ossified carpals. The carpals are flattened. The ulnare is very large and oval. It is more than twice larger than the intermedium, as in advanced protostegids such as *Protostega gigas* (Wieland, 1906) and *Archelon ischyros* (Wieland, 1909), while in *Santanachelys gaffneyi* the ulnare is only slightly larger than the intermedium and has a more rounded shape (Hirayama, 1998). The intermedium has a nearly square shape. The centrale is a small oval element, similar in size to the second distal carpal. The pisiform is large, being slightly larger than the intermedium. A row of five distal carpals is present, the first being the largest. The metacarpals and phalanges are long and dorsoventrally flattened, and all lack movable articulating surface. This is different from *Santanachelys gaffneyi* in which the first and second metacarpals and digits still have movable articulations (Hirayama, 1998).

The length of the digits is 4>3>5>2>1 in all specimens, the fourth one being the longest, as in *Archelon ischyros* and *Protostega gigas* (Wieland, 1906, 1909). Nevertheless, the fourth digit is much longer than the third one in the Nammoura turtles, which is more similar to *P. gigas*, and unlike *A. ischyros* in which the fourth digit is only slightly longer than the third one. In dermochelyids and cheloniids, the third digit is the longest.

The phalangeal formula is 2-3-3-3-3. The second phalanx of the fifth digit has a narrower distal end than other digits. The third phalanx of the fifth digit is disarticulated from the second one, on both sides of MSNM V3933. However they are present, preserved near the second phalanx, on both sides (Fig. 8). This bone is much smaller than the last phalanx of other digits and appears to be clawless. The first four digits are clawed.

In the adult specimen ESC-2, skin impression is preserved around the front and hind limbs, showing the outline of a solid paddle as in living sea turtles. Both front flippers have most of the bones damaged, but their imprints are preserved. The pisiform is nearly as large as the ulnare. There is a rather large and triangular bone

anterior to the pisiform, preserved on both sides. This bone is absent or not preserved in both the hatchling specimens and the juveniles. Such bone is present in one specimen of *Archelon ischyros*, housed in the Natural History Museum of Vienna (Derstler, 1992). It is however absent in the type specimen of *A. ischyros* (Wieland, 1909). The ulnare is smaller than that of MSNM V3933 and is less proximodistally elongated than in the latter. Other carpal elements appear similar to those of MSNM V3933, as well as the length of the digits and the phalangeal formula. The third phalanx of the fifth digit is preserved *in situ* on both sides, although better preserved on the right side. The end of this bone is truncated instead of pointed like the last phalange of other digits and it is situated well inside of the paddle. This indicates that the fifth digit was not clawed (Figs. 6 and 8D-E).

The hatchling specimen Ntu-1 has a relatively larger front flipper than the juveniles and adults. Its length, from the proximal end of the radius to the end of the fourth digit, is about two thirds of the carapace length. The large ulnare is preserved on both sides. There is one distal carpal on the right side and at least two distal carpals on the left side. Other carpal elements are either not ossified or not preserved. The digit length and the phalangeal formula are the same as in juveniles and adults, except that the third phalange of the fifth digit is not present on either side, but this is probably due to preservation. In another hatchling specimen, Ntu-7, the ulnare is the only bone present among the carpals.

Hindlimb (Figs. 1, 6, 7)

The hindlimb is preserved on both sides of MSNM V3933 (Fig. 1) and Ntu-1a (Fig. 7), and on the left side of Ntu-7 (Fig. 3D) and ESC-2 (Fig. 6).

Femur, tibia and fibula: the femur, visible in hatchlings Ntu-1a and in Ntu-7, is shorter than the humerus. Its length in Ntu-1 is about 82 % of that of the humerus. It has a straight shaft and slightly enlarged proximal and distal ends. The fibula and tibia are of roughly the same length, and their length is about 74% of that of the femur in Ntu-1a.

Tarsals, metatarsals and phalanges: tarsals are preserved as imprints in adult ESC-2 on the left side. In this specimen, the astragalus and calcaneum are fused. There are at least three distal tarsals preserved. The metatarsals and phalanges are much shorter than the metacarpals and phalanges of the forelimb. The fifth metatarsal is a large bone and has a semi-circular shape. The first digit is not complete. The second to fifth digits all have three phalanges.

In the juvenile MSNM V3933, the astragalus and calcaneum appear to be distinct bones and three distal tarsals are present on the right side. The first digit has two phalanges. The phalangeal formula, completed on the basis of ESC-2, is 2-3-3-3-3, as seen in most turtles.

In the hatchling Ntu-1, no tarsal is ossified or preserved. The fifth metatarsal is a large and rounded bone, with a posterolateral notch. The first digit has two phalanges and the second to fourth digits have three phalanges. On the fifth digit, although the last (the third) phalanx is not preserved on either side, it must have been present, to judge from the distal end of the second phalanx which is not narrowed.

Discussion

Systematic assignment

The turtle remains from Nammoura are Protostegidae because they exhibit a large star-shaped hyoplastra and hypoplastra, a T-shaped entoplastron with distinct lateral wings, short and curved xiphiplastra and a plastral index over 100 (Hirayama, 1994, 1997, 1998). They are assigned to *Rhinochelys pulchriceps*, a primitive protostegid known from the Albian to the Turonian of western Europe (Collins, 1970; Hirayama, 1997), because they have a large nasal bone, and a laterally expanded and swollen skull roof at the prefrontal level.

The turtle remains from Nammoura include more than half a dozen specimens of various sizes. Four individuals have a carapace length ranging from 16 to 21 mm (Tab. 1). These small specimens are likely hatchlings. The attribution of these hatchlings to *Rhinochelys* is based on the skull features including the overall skull shape and the morphology and arrangement of the skull elements. The medium-sized specimens MSNM V3933 and Ntu-6 are considered juveniles because of their intermediate size, the large carapacial fontanelles, the serrated posterior margin of the carapace and the sutures between the plates, especially those between the peripherals, which are still open. ESC-2 is much larger than MSNM V3933 and Ntu-6, and has a carapace length of 270 mm. It is an adult, with a more elongated carapace, a smooth carapace margin and a reduced carapacial fontanelle. The additional bone on the top of the pisiform in this specimen probably corresponds to a prong on the flipper. This may be an expression of sexual dimorphism. In the living marine turtles, the males have a more developed and curved claw on the front flipper to grip the female's carapace. A prong on the front flipper may have had a similar function. Another male characteristic of ESC-2 is the long tail that extends far beyond the posterior rim of the carapace. The females of living cheloniid usually have a short tail which does not extend beyond the posterior margin of the carapace, or only slightly so. Furthermore, the flatter carapace might be another male character, as seen in some populations of *Chelonia mydas* (Ernst *et al.*, 1994).

The genus *Rhinochelys* was erected by Seeley in 1869 for the type specimen *Chelone pulchriceps* Owen, 1842, a skull from the basal Cenomanian Cambridge Greensand. Since then, several species have been described (for a historical review see Collins, 1970), most of them from England, except for one specimen from France (Moret, 1935), all finds represent isolated skulls. In 1970, Collins reviewed the genus *Rhinochelys*, and recognized three British species and one French species. She suggested that *Cimochelys* from the Albian to Turonian of south-east England, based on shell material, probably represents the postcranium of *Rhinochelys*. This interpretation has generally been accepted by more recent workers (Hirayama, 1997; Hooks, 1998). In a recent review of the chelonioid sea turtles (Hirayama, 1997) and in a revision of the Protostegidae (Hooks, 1998), only one valid species of *Rhinochelys*, *R. pulchriceps*, was recognized.

The skull of MSNM V3933 is very similar to that of *R. pulchriceps* in size and

morphology. However some differences can be observed: in comparison with *R. pulchriceps*, the skull of MSNM V3933 is more elongate, with a smaller nasal, the frontal is smaller with a narrower anterior portion and the parietal is more elongate; the temporal emargination is deeper, being more than half the length of the parietal. In *R. pulchriceps*, the temporal emargination is 'about a third of the length of the parietal' (Collins, 1970).

The shell of the Nammoura turtles is that of primitive protostegid and similar to that of *Cimochelys* in its general morphology, including the carapace outline, roof-shaped cross section, size of carapacial fontanelles, shape of hyoplastron and hypoplastron. This supports the hypothesis that *Rhinochelys* and *Cimochelys* represents the same taxon. However the carapace of the Nammoura turtles slopes less sharply toward the sides and therefore is more flattened. This seems not to be due to post-mortem deformation since both MSNM V3933 and Ntu-6 have a similar shell curvature. Other differences between the Nammoura turtles and *Rhinochelys* (*Cimochelys*) are found in the suprapygal and pygal. The Nammoura turtles have one suprapygal while *Rhinochelys* (*Cimochelys*) has two suprapygals. Furthermore, the width of the vertebral scutes of the Nammoura turtles increase from the second to the fourth, while these scutes have a similar width in *Rhinochelys* (*Cimochelys*). These differences justify the erection of a new species of *Rhinochelys: R. nammourensis*.

Front flipper characters (Figs. 8-9)

Our knowledge on the complete front flipper of protostegids was limited to date to advanced members such as *Protostega gigas* (Wieland, 1902, 1906) and *Archelon ischyros* (Wieland, 1909), in addition to the incomplete but articulated flippers of *Santanachelys gaffneyi* (Hirayama, 1998), *Desmatochelys lowi* (Zangerl & Sloan, 1960) and *Terlinguachelys fischbecki* (Lehman & Tomlinson, 2004), and a few elements in *Calcarichelys gemma* (Hooks, 1998). Wieland (1902, 1906) studied the flippers of *Toxochelys latiremis*, *Archelon ischyros* and *Protostega gigas* and noticed some evolutionary trends in chelonioids, among them the elongation of some digits, and a great and persistent increase in size of the pisiform.

The complete and articulated front flippers of the Nammoura turtles provide important information on their structure and evolution, especially on the proportion between the different elements. The flippers of the Nammoura turtles are more derived than those of *Santanachelys gaffneyi* because the ulnare is more proximodistally elongate and much larger than the intermedium and because all metacarpals and phalanges lack movable articulations. In this respect, the flipper of the Nammoura turtles more closely resembles those of advanced protostegids, such as *Archelon ischyros* and *Protostega gigas*. However, the second digit in the Nammoura turtles remains short, a primitive feature found also in *Santanachelys gaffneyi*.

The comparisons made with other chelonioid sea turtles reveal some interesting features of the family Protostegidae (Tab. 2):

Tab. 2 - Comparison between the front flipper of Protostegidae, Dermochelyidae and Cheloniidae.
Tab. 2 - Confronto tra le natatoie anteriori di Protostegidae, Dermochelyidae e Cheloniidae.

	Protostegidae	Dermochelyidae	Cheloniidae
Ulnare	Very large, the largest among carpals and much larger than intermedium	Large, nearly as large as intermedium	Large, nearly as large as intermedium
Phalangeal formula	2-3-3-3-3	2-3-3-3-2	2-3-3-3-2
Longest digit	4th	3rd	3rd
Elongation of 2nd phalanx of 3rd and 4th digits	no	no	yes
5th digits	Much longer than the 1st digit	shorter than the 1st digit	As long as or longer than the 1st digit

1) Protostegids have a large ulnare, which is clearly larger than the intermedium. The intermedium remains a rather small and short element. This appears to be a synapomorphic feature of Protostegidae. In *Rhinochelys nammourensis*, *Archelon ischyros*, *Protostega gigas* and *Desmatochelys lowi*, the ulnare is twice larger than the intermedium and the latter is as long as wide (*R. nammourensis*, *D. lowi*) or wider than long (*A. ischyros*, *P. gigas*). Although the ulnare of *D. lowi* is not completely preserved, the reconstruction by Zangerl and Sloan (Zangerl & Sloan, 1960) is convincing, being similar to that of the Nammoura turtles. The most primitive protostegid, *Santanachelys gaffneyi*, has the ulnare only slightly larger than the rounded intermedium (Hirayama, 1998). Although the ulnare is slightly larger in modern cheloniids than the intermedium, both intermedium and ulnare are notably elongated bones (Zangerl, 1953b, 1958). The primitive condition is found in *Toxochelys latiremis*, with a small ulnare and intermedium of similar size (Wieland, 1902).

2) There is apparently no reduction in the number of phalanges of the front flipper among protostegids. The phalangeal formula in this group is 2-3-3-3-3, for all taxa for which a complete front flipper is available. However, the third phalanx of the fifth digit of the front flipper is reduced in the Nammoura turtles, which seems not to be the case in *Archelon ischyros* and *Protostega gigas*. Extant cheloniids, as well as *Allopleuron hoffmanni* from the Maastrichtian of Belgium and the Netherlands (Hirayama, 1997; Mulder, 2003) and *Glarichelys knorri* from the Oligocene of Switzerland all have a front flipper phalangeal formula of 2-3-3-3-2 (Zangerl, 1958; Walker, 1973).

3) The length of digits is 4>3>5>2>1 in protostegids, the fourth digit being the longest. Although a similar condition is also found in the most primitive cheloniid, *Toxochelys latiremis* (Wieland, 1902), modern cheloniids and dermochelyids have digit lengths of 3>4>2>5>1, the third digit being the longest, as in the freshwater turtle *Pseudemys* (Walker, 1973). The elongation of the third to fifth digits of manus and

pes is considered as a synapomorphic feature of Chelonioidea (Hirayama, 1994), a character already recognized by (Wieland, 1909). Zangerl (1953b) pointed out that the second to fourth digits of the front flipper are greatly elongated in cheloniids. The fifth digit of cheloniids is generally short, being shorter than the second one and only slightly longer than the first digit. In protostegids, the fifth digit is greatly elongated and is much longer than the second digit.

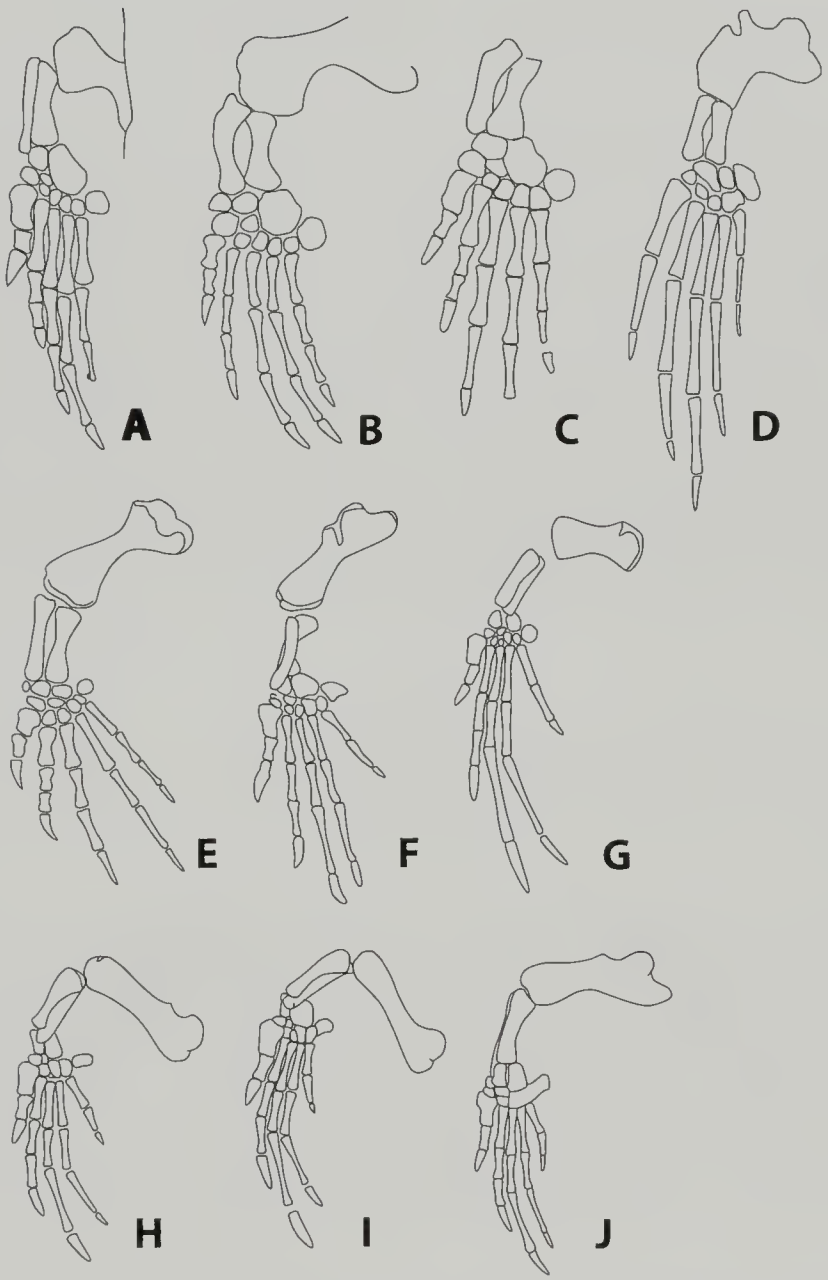

Fig. 9 - Comparison of front flipper of protostegids, cheloniids and dermochelyids (Confronto tra le natatoie anteriori di protostegidi, cheloniidi e dermochelyidi). A) *Rhinochelys nammourensis*; B) *Archelon ischyros* after (da) Wieland, 1909; C) *Protostega gigas* after (da) Wieland, 1906; D) *Dermochelys coriacea*; E) *Toxochelys latiremis* after (da) Wieland, 1902; F) *Allopleuron hoffmanni* after (da) Hirayama, 1997; G) *Glarichelys knorri* after (da) Zangerl, 1958; H) *Eretmochelys imbricata* after (da) Zangerl, 1958; I) *Lepidochelys kempi* after (da) Zangerl, 1958; J) *Chelonia mydas* after (da) Zangerl, 1958. All specimens are showing as being from the left side for easier comparison (Per rendere più immediato il confronto tutti gli esemplari sono raffigurati come se fossero visti dal lato sinistro). Not to scale (Non in scala).

The great elongation of the third and the fourth digits in advanced cheloniids, including all extant species, as well as *Allopleuron hoffmanni* and *Glarichelys knorri*, is accomplished by a significant elongation of the second phalanx, especially that of the third digit. This results in the second phalanx of these digits being clearly longer than the first phalanx of the same digit. In dermochelyids and protostegids, the second phalanx of the third and fourth digits is roughly as long as the first one. However the primitive cheloniid *Toxochelys* has a digit configuration similar to that of protostegids (Wieland, 1902). This suggests that the protostegids might retain the primitive digit configuration of Chelonioidea.

Hatchling and juvenile characters

The hatchlings Ntu-1, Ntu-7, Ntu-8 and ESC-3 are rather different from the juvenile and adult specimens in their shell morphology. In addition to having very large skulls and front flippers in respect to the shell, as in living cheloniids, other presumed hatchling characters include: the costal plates blade-like and separated from one another by the fontanelle along their entire width; the central plastral fontanelle very large and extending the full width, no contact between the hyoplastra and hypoplastra at the hatchling stage. Star-shaped hyoplastron and hypoplastron which are as long as wide occur later, being present in juveniles. In hatchlings, finger-like prongs are present only on the medial margin. In addition, the anterior curvature of the radius occurs progressively, it is not present or barely visible in hatchlings and juveniles, but well marked in adults.

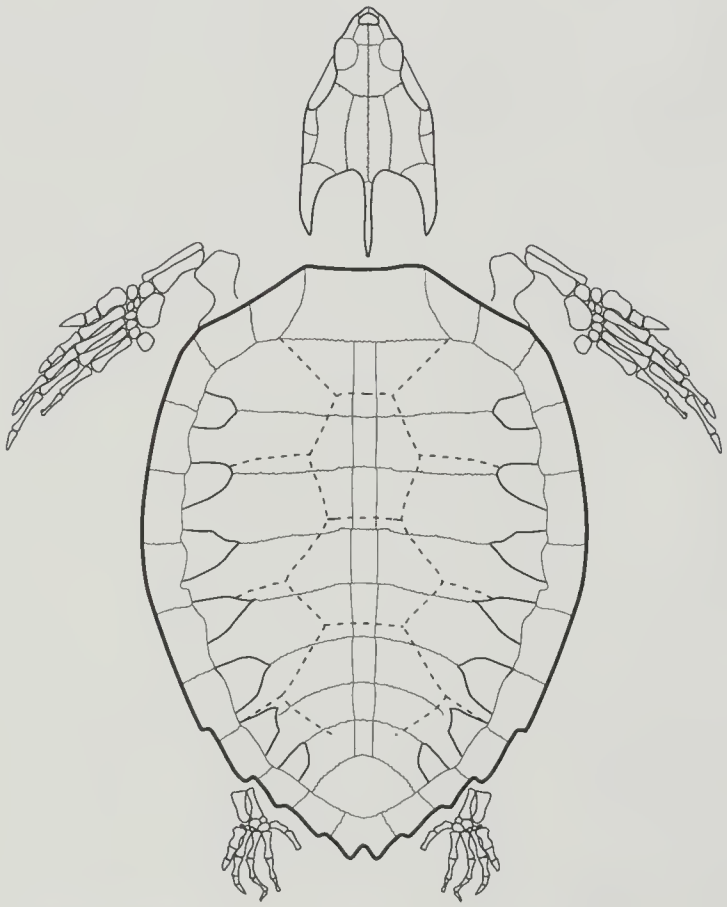

Fig. 10 - *Rhinochelys nammourensis* n. sp.: reconstruction (riscostruzione).

Conclusion

The Cenomanian Nammoura locality has yielded the most complete known *Rhinochelys* specimens, which belong to a new species, *Rhinochelys nammourensis*. Almost complete and articulated skeletons, hitherto unknown for this genus, support the hypothesis that *Rhinochelys*, based on skulls, and *Cimochelys*, based on shells, belong to the same taxon. The hatchling, juvenile and adult specimens of the same taxon, reported for the first time among protostegids, reveal important ontogenetic characters. The complete and articulated front flippers provide additional plesiomorphic and synapomorphic features for the family Protostegidae relative to Dermochelyidae and Cheloniidae. In addition to the synapomorphic features of the humerus and radius already mentioned by Hirayama (1992, 1994, 1997), the protostegids have a extraordinarily large ulnare. However, the front flipper of protostegids appears to retain the primitive digit configuration of chelonioids, in the relative length of the digits and phalanges and in the absence of reduction of the number of phalanges, which closely resembles the condition of the primitive cheloniid *Toxochelys latiremis*.

During the Cenomanian, Lebanon and the whole Arabic peninsula were part of the African continent, on the northern part of Gondwana. The Nammoura turtles are therefore the first Protostegidae to be recorded from the African-Arabian continent. The distribution of the genus *Rhinochelys* is therefore extended from the Anglo-Parisian Basin and northern Tethys southward to the eastern part of the Tethys. The discovery of relatively abundant neonate turtles probably indicates that the locality was not far from the nesting site.

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